POST-INGESTIVE UTILIZATION OF PLANT BIOMASS AND NITROGEN BY LEPIDOPTERA: LEGUME FEEDING BY THE SOUTHERN ARMYWORM

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Abstract.—Polyphagous southern armyworms, *Spodoptera eridania,* are extremely efficient at assimilating ingested biomass and nitrogen in foliage of forage legumes. Variable efficiencies of processing the digested food (E.C.D.) were observed, however, and these differences reflect metabolic costs which may be related to biochemical factors mediating varietal differences in host plant resistance to other kinds of insects. Armyworms are apparently able to compensate for low conversion efficiencies with increased consumption rates such that their relative growth rates (mg. gained/ mg. tissue/day) are virtually independent of digestive efficiency. In fact, larval growth rates of southern armyworms on these 15 legume varieties were among the greatest observed in a comparison with 22 other species of Lepidoptera in 140 similar feeding experiments. It appears that the combination of high leaf water content (80–91%) and high nitrogen content (4.2– 5.5% dry) of legume foliage are key factors permitting such growth. Allelochemics such as coumarin or the various saponins known to be present in these legumes were ineffective "barriers" to larval feeding and growth of armyworms in no-choice situations.

Introduction

The relative post-ingestive roles of allelochemics and plant nutritional quality (e.g. leaf water content and leaf nitrogen content) in determining larval growth efficiencies have been analyzed for 22 species of Lepidoptera larvae feeding upon a variety of normal foodplant species (Scriber, 1978a). Foodplants used in these experiments ranged from trees (with leaf-water and nitrogen contents of 50% and 1%, respectively) to various groups of forb species with leaf-water typically in the range of 80% to 90% and nitrogen content ranging from 1.5% to 6.0%. In addition to a range of nitrogen concentrations provided by mature forb leaves, the Apiaceae (= Umbelliferae) (Kingsbury, 1964; Hegnauer, 1971) and the Cruciferae (Kjaer, 1974; Slansky and Feeny, 1977; and Chew, 1975) were chosen because of the unique array of allelochemics encountered in the various species. In the study to be reported here, a variety of species of the Leguminoseae were selected because of their high nitrogen as well as high water content, and also for the assortment of insect resistant genotypes (cultivars) which were
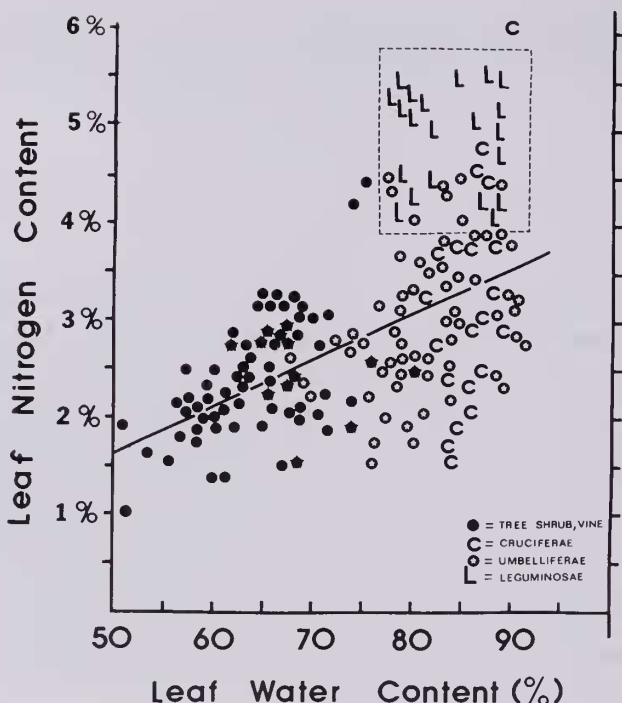
Fig. 1.   The relationship of mean leaf nitrogen content and mean leaf water content of plants used for feeding experiments with various Lepidoptera. In this study the 15 legume varieties are indicated ("L") for comparison with 21 Cruciferae varieties ("C"), various Umbelliferae (starred), and additional vine, shrub, and tree species (solid circles) from experiments reported by Scriber (1978a). The six additional legumes are described by Scriber (1978b).

available for analyzing the relative growth suppressive effects upon the po-lyphagous southern armyworm, *Spodoptera eridania* (Cram.).

The possible importance of leaf water content in determining the larval growth of certain tree-feeding Lepidoptera has been described by Scriber (1977, 1979a). A comprehensive study of various swallowtail butterfly (Pa-pilionidae) and silkmoth (Bombycoidea) species has revealed a striking cor-relation between larval growth and growth form of the foodplants (Scriber and Feeny, 1979). Leaf water content appears to provide a general indica-tion of the larval performance to be expected from a variety of species of Lepidoptera of different sizes and different degrees of feeding specialization (Scriber 1978a). Just as the variance from the regression on leaf water of nitrogen content of mature leaves increased above 75% leaf water content (Fig. 1), so does the variance in larval performance (Scriber, 1978a; Scriber and Feeny, 1979). Larval performance (the consumption, assimilation, and

conversion of plant biomass and nitrogen for tissue growth) of forb feeders is generally much better than tree leaf feeders, and larval growth rate (mg. gain/mg. dry tissue/day) of herb feeders is generally $2\times$–$6\times$ that of tree feeders.

Although the patterns of biomass and nitrogen accumulation rates between tree- and forb-feeding larvae are rather striking (Scriber and Feeny, 1979), we do not know the relative contributions of low nitrogen, high fiber, high tannin or other factors which could be involved in suppressing larval growth rates upon mature tree leaves. Furthermore, seasonal variations in nutritional quality of tree leaves are certainly of prime concern to lepidopteran herbivores (see Feeny, 1970, 1976; Rhoades and Cates, 1976). Seasonal variation in nutritional quality of forbs is also a very important factor determining larval growth rates and also may be more important than qualitative plant allelochemics in determining utilization efficiencies of the Umbelliferae by 'adapted' herbivores (Finke, 1977). Of course, nutritional quality will be much less important when qualitative (behaviorally deterrent) allelochemics are encountered by "unadapted" herbivores (see Erickson and Feeny, 1974; Feeny, 1975; Blau et al., 1978).

Any limiting effects of leaf water would presumably be less obvious for larvae feeding on plant tissues with 75–90% water content (e.g., forbs). It may thus be more likely that leaf nitrogen or allelochemic content would play more significant roles in determining the post-ingestive utilization of forb tissues for larval growth. Slansky and Feeny (1977) analyzed utilization of various Cruciferae species by larvae of an 'adapted specialist,' *Pieris rapae* L. They suggest that nitrogen is indeed in limiting supply (81–90% leaf water content) and that larvae increase their feeding rates on plants which are low in nitrogen content in order to maximize the nitrogen accumulation rate (N.A.R. = Nitrogen Consumption Rate $\times$ Nitrogen Utilization Efficiency). The consumption rate of nitrogen was apparently increased up to a point beyond which declining nitrogen utilization efficiency (N.U.E.) offset the gain. It was suggested that consumption rate on any particular crucifer species would be adjusted to the lowest value at which maximal N.A.R. could occur. Although at least 19 different glucosinolates were reported from leaves of these foodplants, there was no detectable correlation between larval growth rate and these patterns of allelochemics. Perhaps the importance of nitrogen in this study of Cruciferae-adapted larvae may have obscured any subtle allelochemic effects.

The independent roles and synergistic effects of leaf-water content, leaf nitrogen and allelochemics on larval growth are very difficult to assess. The use of allelochemics in artificial diet studies (Reese and Beck 1976a, b, c) or plants which are polymorphic for allelochemics (Scriber, 1978b) allow some control of variables. Regulation of diet water content in artificial diets (Reese, 1977; Reese and Beck, 1978) or in natural foodplant leaves (Scriber,

1977) permits additional assessment of the relative importance of water in relation to other aspects of the diet. Fertilization to increase plant nitrogen content generally results in increased leaf water content as well (see Slansky and Feeny, 1977), and may not permit one to distinguish between effects to be attributed to these two variables.

It was the intent of the present study to attempt an assessment of the effects on larval growth of various plant characteristics of the Leguminosae family. In this study, the leaf-water content was relatively high (80–91%) and the plant nitrogen content was also generally high (4.2–5.5%). It was thus hoped that any differences in larval performance on 15 forage cultivars would not primarily be reflections of leaf-water and nitrogen limitations, but instead might reflect the more subtle post-ingestive effects of various bio-chemical factors implicated in host-plant resistance.

Methods and Materials

Fifteen Legume species selected and bred for agronomic qualities and insect resistance were fed to larvae of the southern armyworm (*S. eridania*). Growth performances on alfalfa varieties (Apollo, Arc, Culver, Kanza, MSA-CW3-AN3, Ranger, Riley, Team, Vernal, and Weevlcheck) were com-pared and contrasted with bird's foot trefoil, *Lotus corniculatus;* red clovers (Arlington and Lakeland); white clover; and yellow blossom sweet clover in these bioassays. Glasshouse-grown seedlings about 12 inches in height were used.

Consumption rates, assimilation efficiencies, conversion efficiencies and relative accumulation rates of biomass and nitrogen were determined for larvae via gravimetric methods (see Waldbauer, 1968; and Scriber 1977, 1978b for methods). These values were compared to those for other Lepi-doptera as reported in Scriber (1978a), and in the figures presented here, the regression lines are calculated based on the means for the previous 140 experiments and do not include the 15 legume experiments.

Environmental conditions were vitually identical for all experiments re-ported (16:8 hr. photo: scotophase with a corresponding temperature regime of 23:19 C°). Included in these comparisons are experiments of Slansky and Feeny (1977) and Finke (1977) as well as those of Scriber (1975, 1978a, 1978b, 1979b) and Scriber and Feeny (1979).

Results and Discussion

As larval performance is surveyed over a range of foodplants from trees (with leaf-water contents of 50–75%) to forbs (with leaf-water contents of 75–95%), it becomes obvious that herb leaves are generally consumed more rapidly and converted to larval biomass more efficiently than tree leaves (Scriber 1978a). Legumes analyzed in this study support these general pat-
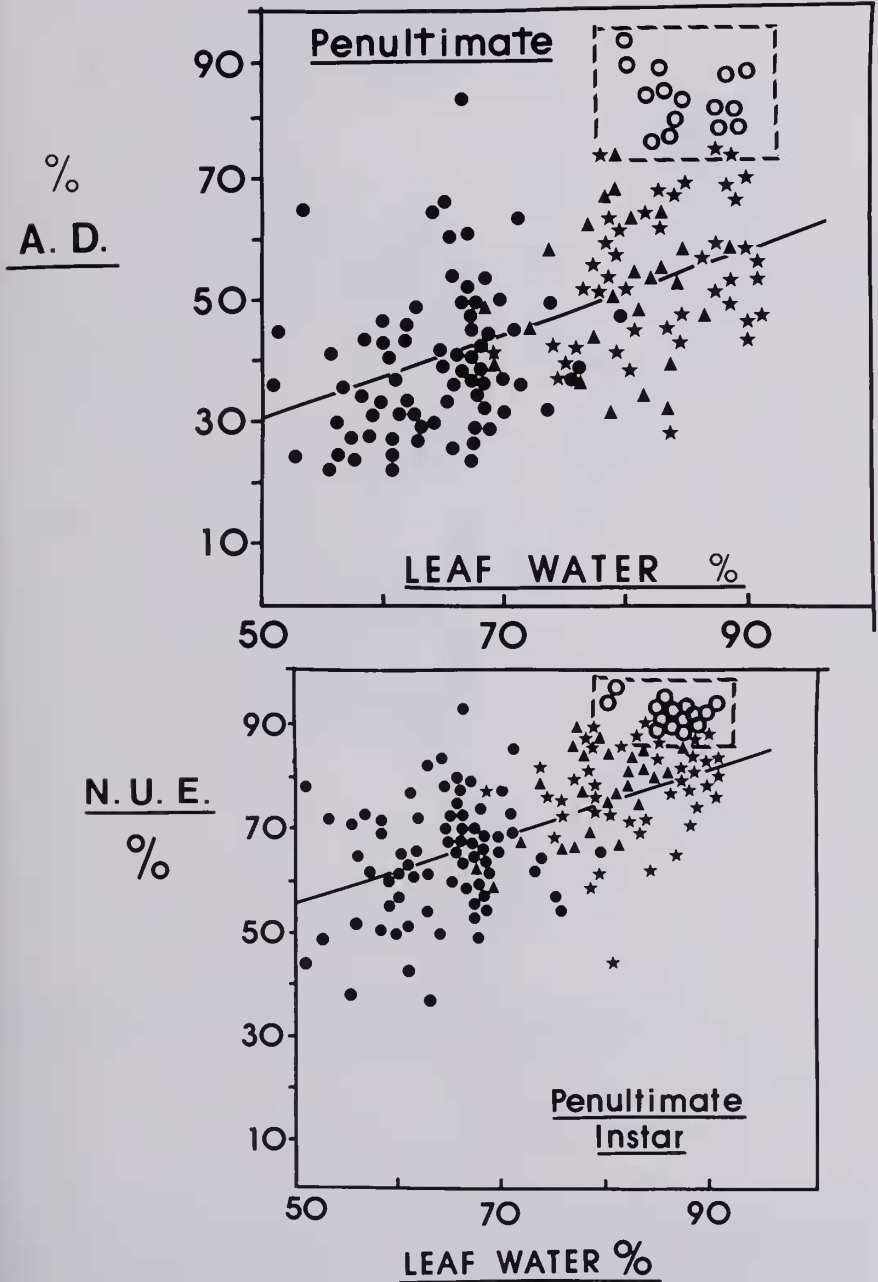
Fig. 2. Approximate digestibilities (Fig. 2a) and nitrogen utilization efficiencies (2b) of 22 species of lepidoptera in their penultimate instar as a function of leaf water content of their foodplants (n = 155). Trees, shrubs and vines are indicated by a solid circle, forbs are indicated by stars and triangles, and legumes by open circles (cf. Scriber, 1978a).
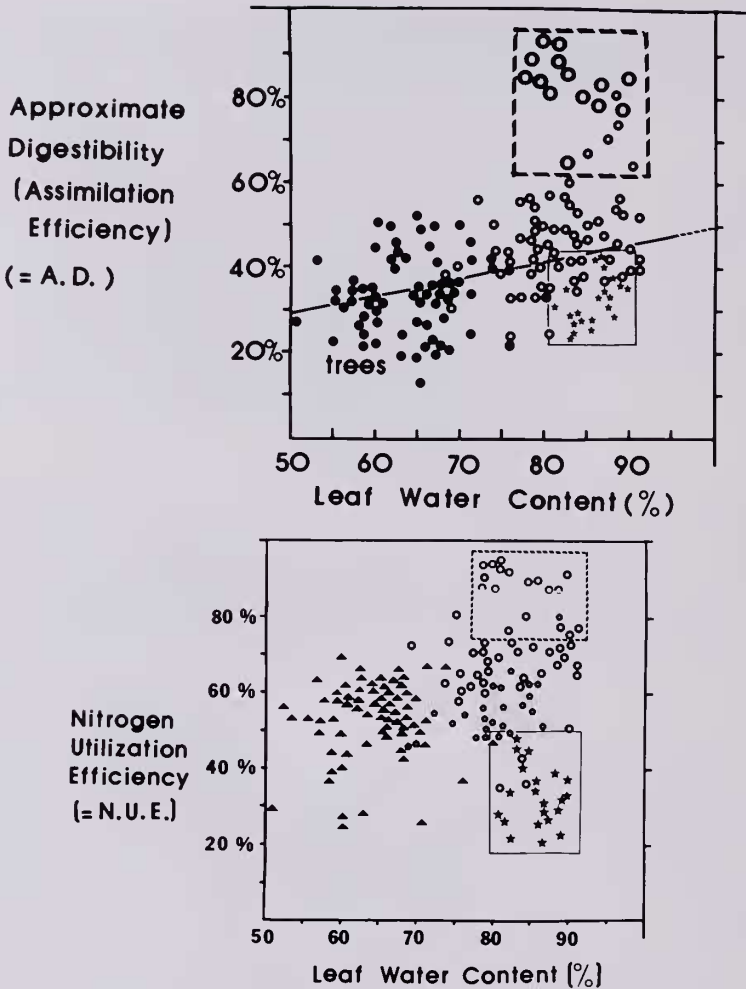
Fig. 3. Approximate digestibilities (Fig. 3a) and nitrogen utilization efficiencies (Fig. 3b) of final instar Lepidoptera as a function of leaf water of their foodplants (n = 170 experiments). The legume experiments are indicated by open circles and the Cruciferae by stars (cf. Scriber, 1978a). Solid symbols represent tree species.

terns, but more striking was the efficiency with which larvae were able to assimilate legume biomass and nitrogen in relation to penultimate instar lepidoptera in 140 other feeding experiments. The biomass assimilation efficiency or approximate digestibility (A.D.) of legumes by penultimate instar larvae ranges from 76 to 94% (Fig. 2a), and nitrogen utilization efficiencies (N.U.E.'s) from 89 to 96% (Fig. 2b). This pattern was also observed for
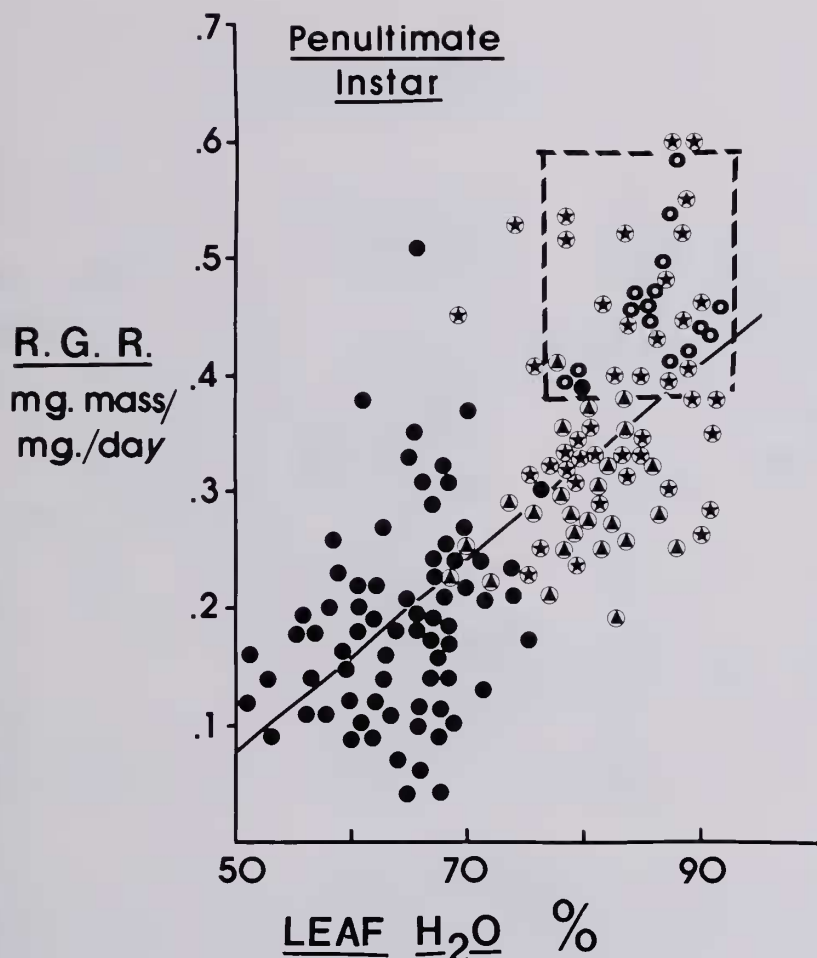
Fig. 4. The relative growth rates of penultimate instar Lepidoptera larvae as a function of the average leaf water content of the foodplant reared upon. The regression line was calculated previous to the inclusion of the 15 legume experiments (open circles).

legume-fed larvae in the final instar. The A.D.'s ranged from 64–92% and N.U.E.'s from 76–95% (Figs. 3a, 3b).

When performance data of final instar *Pieris rapae* on various Cruciferae (Slansky and Feeny, 1977) were compared to those of Umbellifer- and Legume-feeding lepidoptera, it appears that the Cruciferae may uniformly restrict the assimilation of biomass (A.D.) and nitrogen (N.U.E.) by *P. rapae* larvae (Fig. 3a and 3b respectively). While low efficiency of assimilating nitrogen and biomass could be related to nutritional qualities of the Crucif-
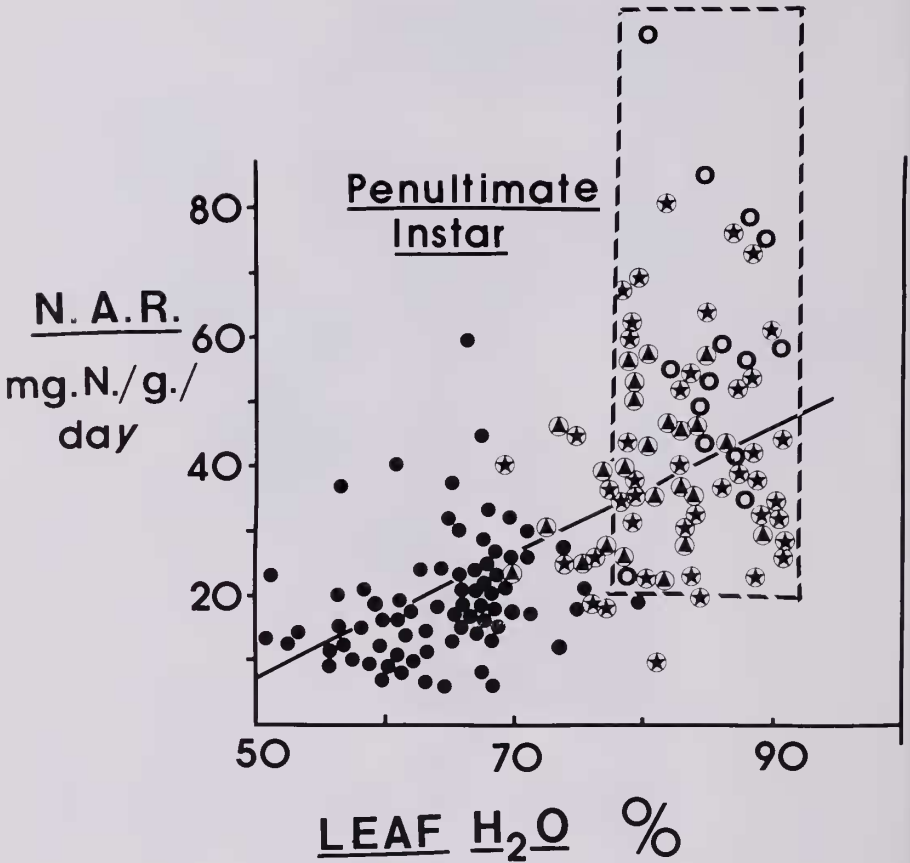
Fig. 5.   The nitrogen accumulation rate (N.A.R.) of penultimate instar larvae as a function of leaf water content. Symbols represent the same plant types as in figure 2 and figure 4.

erae, perhaps glucosinolates should also be considered. These allelochemics may thus have suppressive effects even upon Cruciferae-adapted specialists. While growth of *P. rapae* is not affected even by artificially high concentrations of allylglucosinolate (Blau et al., 1978), it appears that the larvae are able to compensate for low efficiency of assimilating crucifer leaf tissues by increased consumption rates (Slansky and Feeny, 1977; cf. Scriber, 1978a).

Umbellifer-feeding specialists (*Papilio polyxenes* and *P. zelicaon*) studied by Scriber and Feeny (1978) and Finke (1977) exhibited intermediate efficiencies in relation to *P. rapae* on Cruciferae and *S. eridania* on Leguminosae (Fig. 3a and 3b). Specialized forb feeders such as these species of
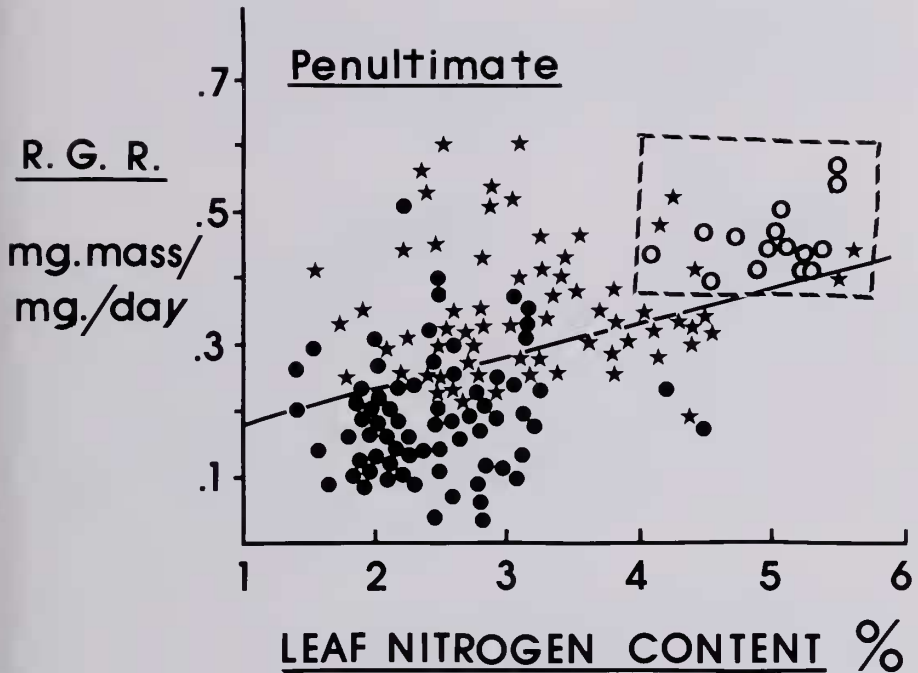
Fig. 6. Relative growth rate of penultimate instar larvae of 22 species of Lepidoptera as a function of leaf nitrogen content of their foodplants. Tree, shrub and vine plants are indicated by solid circles, forbs by stars, and legumes by open circles (See also Scriber, 1978a).

Umbellifer-feeding Lepidoptera grew at rates $2\times$–$3\times$ those of the 18 species of tree, shrub and vine feeders (Fig. 4). Larval growth rates (R.G.R., Fig. 4) and nitrogen accumulation rates (N.A.R., Fig. 5) for the polyphagous *S. eridania* were also $2\times$–$3\times$ greater than tree feeders as a group, suggesting that plant quality rather than degree of feeding specialization may be the more important influence.

Compared to the 22 species of Lepidoptera (Scriber, 1978a), larval growth rate is very fast for these armyworms on legumes. High nitrogen content (Fig. 6) as well as high water content (Fig. 4) is certainly a key contributing factor. While efficiencies of assimilating biomass and nitrogen are high for larvae on all of these forage legumes (Fig. 2 and 3), the efficiency of conversion of digested (assimilated) biomass (E.C.D.) was extremely variable. The low efficiencies of biomass conversion on Team (18.9%), Arc (24.1%) and Culver (29.8%) alfalfa varieties reflect greater metabolic costs for larvae than observed for other varieties (e.g. larvae fed Vernal and Apollo alfalfa had E.C.D.'s = 76.6% and 68.3% respectively, with 71.3% on yellow blossom sweet clover).
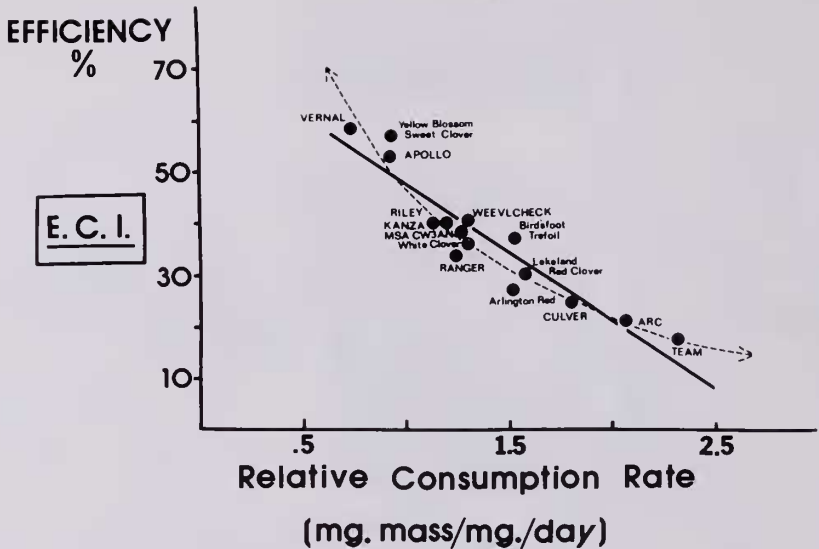
Fig. 7. The gross efficiency of growth (E.C.I. = A.D. × E.C.D.) as a function of the relative consumption rate (R.C.R.) of plant biomass. Each symbol represents the experimental mean values obtained for penultimate instar *S. eridania* larvae on a particular legume variety. (r = .937; n = 15 for linear regression Y = 74.2 − 26.6X).

Why are certain genotypes more costly to process (in terms of assimilated energy and biomass) than others? Team, Arc and Culver alfalfa have been bred specifically for insect resistance to alfalfa weevil, aphids and meadow spittlebugs (Wilson and Davis, 1960; Barnes et al., 1970 and 1977; Sorensen et al., 1972), while Vernal and Apollo have been bred primarily for agronomic qualities and yield potential in Wisconsin (Rohweder et al., 1978). Concentrations of saponins, coumarin, cyanogenic glycosides and nitrates were not determined in this study. However, allelochemical variations between varieties can influence resistance to many insects (Horber, 1972; 1974; Manglitz et al., 1976; Pederson et al., 1976), and might be responsible for some of the variation metabolic costs experienced by armyworm larvae in the present study. Induction of the mixed function oxidase detoxication activity in *S. eridania* can be very rapid (Brattsten et al., 1977); however, it is premature to suggest that possession or operation of these enzyme systems is directly related to differential metabolic costs as measured here.

Nonetheless, polyphagous southern armyworm, *S. eridania,* is apparently able to compensate for the low efficiencies of conversion (i.e., high metabolic costs) on certain legume varieties by increased rates of food consumption (Fig. 7). This allows rapid growth in spite of the need to process a variety of potential allelochemics in legume tissues. This 'power and efficiency'

trade-off (Odum and Pinkerton, 1955; Fig. 7) has not been observed for tree-feeding Lepidoptera (Scriber, 1978a). It has been suggested that in these cases low leaf water content may be a fundamental efficiency limiting factor and that increased consumption rates would perhaps only aggravate the problem (Scriber, 1977).

Conclusions

While some insects are effectively repelled, deterred or suppressed by different biochemicals in the 15 legumes used in this study, the southern armyworm is able to feed and grow successfully. Significant differences in metabolic costs of processing and converting plant biomass were reflected by E.C.D.'s (efficiency of conversion of digested food), which ranged from less than 20% to more than 75% on certain varieties. Larvae were, however, able to "compensate" by increasing their rate of consumption where efficiencies were low. It is suggested that this compensatory mechanism of maintaining larval growth rates near their maximum would be successful primarily where leaf water is not a limiting factor.

Acknowledgments

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